

Keep it simple? Dispersal abilities can explain why species range sizes differ, the case study of West African amphibians

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ABSTRACT

A well-known positive correlation between niche breadth and range size exists across a number of animal and plant taxa. A relatively more simple explanation, range size being connected to differing dispersal abilities, was recently presented for passerine birds. Unfortunately, respective datasets are not easily available for other taxonomic groups. We circumvented this problem by developing a simple dispersal index, incorporating niche information (body size, litter size, preferred habitats of adults and offspring, ecotype of adults) which can be collected straightforwardly for most animal taxa. We tested this dispersal index for species which are generally considered poor dispersers, amphibians. Our results from West Africa revealed a positive correlation between the dispersal index and range size ($p < 0.001$). Our index can easily be transferred to and tested with other taxa. Furthermore, our results suggest one possible way of integrating information on dispersal abilities in niche modelling (distribution modelling) processes which assess the impact of climate change on future species distributions.

1. Introduction

The niche of a species is generally described as a hyperdimensional space, comprising all environments and resources which influence its survival and performance (Hutchinson, 1957) and which are in turn influenced by the species (Leibold, 1995; see also Chase and Leibold, 2003 for a review and refinement of the niche concept). The hypothesis that species with broader niches should have larger geographic ranges was already reviewed more than 30 years ago (Brown, 1984) and more recently confirmed across a wide range of animal and plant taxa (Slatyer et al., 2013). However, the niche of a species is determined by a large variety of different abiotic and biotic factors, the interactions between these factors and with the species, and all may act on different spatial and temporal scales. In addition, large intraspecific variations may occur in the direction and strength of certain factors (Morrison and Hero, 2003). Therefore, the niche of a species is a complex concept which is difficult to measure unambiguously. Thus, it is not surprising that the generalization showing a positive correlation between niche breadth and geographical range was not universally accepted (see Slatyer et al., 2013).

Nevertheless, the discussion why some species do have larger range sizes than others is still on-going and earlier studies have discussed a

variety of less complex explanations than niche breadth, investigating only parts of the niche, e.g. dispersal ability (e.g. Lester et al., 2007; Estrada et al., 2016). However, Lester et al. (2007) failed to find evidence for a relationship between range size and dispersal ability in various marine taxa whereas Estrada et al. (2015), beside other factors, detected a positive correlation between dispersal potential and range size in plants. One major problem of studies investigating dispersal abilities is that comprehensive data is often lacking because no universal measurement of dispersal ability exists; neither across nor even within most taxonomic groups. A number of indirect measures to assess dispersal have been used, e.g. distance travelled (e.g. Spieler and Linsenmair, 1998), genetic exchange (e.g. Szymura and Barton, 1991) and evolutionary time (e.g. Pigot et al., 2012; see also review by Smith and Green, 2005).

The rare exception in this general lack of knowledge on dispersal are flying vertebrates. For bats a meta-analysis revealed that good disperser have a higher flight speed and migrate seasonally (Burns and Broders, 2014). Similarly, in birds, individual marking, in the form of ringing, has a long tradition, spanning large geographic areas and numerous taxa, amounting in decades of data (e.g. see Laube et al., 2013). An exceptional dataset of European passerine birds showed that dispersal ability, measured as the ratio between Kipp's distance ("distance

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between the tip of the first primary to the tip of the wing") and bill depth (height at base), has an influence on the species' range sizes (Laube et al., 2013); meaning that birds with a better dispersal ability have larger distribution ranges. However, although birds do have ideally suited data sets, they are also exceptional dispersers due to their ability to fly, making dispersal comparatively easier for them than for other groups. We are not aware of similar comprehensive data sets for any other group of animals. Furthermore, the study by Laube et al. (2013) also exemplifies a major bias in the existing dispersal literature: the majority of studies deal with plants, terrestrial endothermic vertebrates, butterflies and temperate regions (Europe or North America; Estrada et al., 2016).

Lead by the corroboration that in general niche breadth and range size are positively linked (see Slatyer et al., 2013), as well as the findings that dispersal ability provided a more frugal explanation for range-sizes in passerine birds (see Laube et al., 2013), we herein developed a simple universal measure of dispersal ability and investigated the question whether there is a correlation between this index of dispersal abilities and range sizes? In particular we were interested in the nature of this relationship, if contrary to the majority of studies, one looks at tropical, non-volant ectotherms, i.e. amphibians. These exhibit a high degree of habitat specificity and due to a number of other characteristics, are generally considered having poor dispersal abilities. To test this question we used a comprehensive data set of niche characteristics of West African amphibians, a well-defined area with a high species diversity and a high fragmentation of forests, which revealed that amphibian dispersal abilities are positively correlated with range sizes.

2. Material and methods

2.1. Amphibian data

Our geographic region is a well-defined African biome and its definition included all countries west of Cameroon and south of the Saharan desert, herein termed West Africa (see Penner et al., 2011). We used a dataset of West African amphibians where taxonomic work over the last two decades resolved potential taxonomic issues and resulted in a total of 192 validated taxonomic units which are either described species or considered confirmed candidate species (compare to Vieites et al., 2009). For the present work, environmental niche models (ENMs) were calculated for 176 of these taxa (similar to the approach by Herkert et al., 2016; see Appendix S1 for more details).

2.2. Dispersal ability index

Amphibians are generally considered having low dispersal abilities (e.g. Sinsch, 1990; Blaustein et al., 1994; Duellman and Trueb, 1994) but probably with high interspecific variation (e.g. Marsh and Trenham, 2001). Overall, data on dispersal abilities for amphibians are scarce and have to be gathered via extensive and expensive methods. For West Africa data exists only for two species (*Hoplobatrachus occipitalis*; Spieler and Linsenmair, 1998; *Phrynobatrachus guineensis*; Sandberger et al., 2010). It is impossible to gather such data for the majority of species within a reasonable time. Therefore an indirect measure has to be used. We collected niche characteristics for all taxonomical units ($n = 176$; see S1), consisting of a variety of measured and estimated parameters which we considered essential for the dispersal abilities and which were easy to collect.

2.3. Snout-vent length [SVL; measured in millimeters]

Larger frogs are less vulnerable to predation (Chelgren et al., 2008), desiccation (e.g. Jameson, 1956; Semlitsch, 1981; Rothermel and Semlitsch, 2002) and travel larger distances (e.g. Goater et al., 1993; Beck and Congdon, 2000). Thus, larger frogs should have dispersal

advantages. The assumption that dispersal is not uniform, e.g. juveniles (e.g. Dole, 1971; Breden, 1987; Berven and Grudzien, 1990), males (e.g. Lampert et al., 2003) or females (e.g. Austin et al., 2003; Palo et al., 2004) being the main dispersal unit, remains untested for West African species. For most species it remains also unknown at which age they start reproducing, thus the distinction between juveniles and adults is not always straightforward. It is also mostly unknown how far size is correlated with age, a long life span is reported as being positively correlated with range size (Trakimas et al., 2016). Therefore, the mean SVL of adults can be seriously hampered by the inclusion of small, possibly immature frogs. To avoid that, we recorded only the maximum sizes for males and females. The dispersal index used the size of the larger sex (usually the female).

2.4. Clutch size [Cl; assigned to six categories]

Fecundity has been shown to be an important variable in explaining range size variation in amphibians (Trakimas et al., 2016). We recorded the number of eggs a single female may deposit during one breeding event either from own data or from the literature. Clutch sizes were grouped in four categories < 20 eggs (i), 21–100 (ii), 101–1000 (iii), > 1001 (iv). For reasons of simplification, we assumed that predation on eggs and tadpoles are comparable throughout species and thus having larger clutches is a dispersal advantage. The four categories were taken into account by integrating the multiplication factor of 1 (i), 2 (ii), 3 (iii) and 4 (iv), respectively into the dispersal index.

2.5. Preferred habitat of adults [Ad-Hab; six categories]

The habitat preferences of adults for all species were assigned to six categories: primary forests (PF), secondary forests (SF), forest edges and clearings (FE), highland savannahs (HS), lowland moist savannahs (LSM) and lowland dry savannahs (LSD); multiple assignments were possible. Forests, both primary and secondary, are heavily fragmented in West Africa and very few large forest patches still persist (e.g. Mayaux et al., 2004; Hansen et al., 2013). We assumed that forest dependent species very rarely cross savannahs, whereas savannah species can cross forested habitats along roads and other anthropogenic openings or even move within forest. The latter is supported by data which revealed savannah species deep inside rainforest, on so called inselbergs (Schorr, 2003). In West Africa, highland savannahs are naturally fragmented. Thus FE, LSM and LSD were included in the dispersal index with the multiplication factor two, PF, SF and HS with the factor one.

2.6. Preferred ecotype of adults [EcoT; four categories]

Species were classified in four categories: terrestrial, arboreal, fossorial and aquatic. We assumed that terrestrial amphibians have a dispersal advantage over the remaining three classes because their habitat is, relatively seen, more "continuous" than for the other three categories. Therefore, this category received a multiplication factor of two, while the others received one of one.

2.7. Larval habitat [L-Hab; five categories]

The habitat preferences of amphibian larvae, tadpoles, were assigned to five categories related to their dependence on water: terrestrial (i; including life birth) and stagnant permanent (ii), stagnant temporary (iii), flowing lowland (iv), flowing mountain (v) aquatic habitats. We considered the first three categories (i, ii & iii) as facilitating dispersal and the remaining two as limiting dispersal. The reasoning was that suitable breeding habitats are generally scarce, giving a dispersal advantage to species who are independent of water (i) and who can use the most abundant water bodies – stagnant ponds (ii & iii), at least during the rainy season and in our study area. Smaller flowing waters may dry out in drier areas, larger ones may contain predatory

fish and both are less abundant than stagnant waters. Thus, the facilitators multiplied the index by two, the remaining (iv, v) by one.

The index was normalized to range from 0 to 1. Thus our simple (standardized) dispersal ability index (DI) has the following formula:

$$\text{DI} = \text{SVL} \times \text{Cl} \times \text{Ad-Hab} \times \text{EcoT} \times \text{L-Hab}. \quad (1)$$

2.8. Range size

In order to keep distributional bias at a minimum we did neither use estimated distribution polygons nor similar proxies (e.g. areas of occupancy, estimates of occurrence). Instead we extrapolated occurrence records with the aid of an ENM algorithm (Maxent) to infer a more objective range sizes for each individual species. ENM is a statistical modelling technique and in our case contrasts environmental parameters from known occurrences against randomly created “pseudo-absences” by maximizing entropy (Phillips et al., 2004, 2006; Phillips and Dudík, 2008; Elith et al., 2011). The method is well suited when absences are unknown and when only low numbers of occurrences exist (e.g. Elith et al., 2006; Heikkinen et al., 2012). ENMs were calculated for the whole African continent, cut at the 10 percentile threshold and manually corrected for biogeographic barriers. The ENMs employed 18 environmental parameters on a 30 Arc second grid (see Appendix S1, S2 for details).

2.9. Niche breadth

We calculated niche breadth for the environmental niche only. First we run a spatial PCA of all 18 environmental parameters (see above; using ESRI ArcGIS 10.0). Afterwards we extracted the maximum, minimum and mean values as well as standard deviations for three PCA axes over the modelled range of all species.

2.10. Statistics

To test the correlations between dispersal, range sizes and niche breadths we calculated multiple Spearman-rank correlation tests with a Bonferroni correction (R software 3.0.1 (2013); ltm package, Rizopoulos, 2006). The categorical nature of our data set (see above) did not allow for any parametric tests.

3. Results

There was a highly significant correlation between mean niche breadth, measured as environmental variance throughout the range of a species, and range size [Spearman-rank correlation with Bonferroni correction for the first two PCA axis [see Fig. 1; $p < 0.001$; rho = -0.608 (PCA1); $p < 0.001$; rho = -0.581 (PCA2)]. There was also a correlation between the variance of the environmental niche (standard deviation) and the range sizes for the third PCA axis [see Fig. 1; $p < 0.001$; rho = 0.538]. The explained variation was 87.1% (PCA1), 11.9% (PCA2) and 0.9% (PCA3). The correlation between our dispersal ability index and range sizes was highly significant (Spearman-rank correlation, $p < 0.001$; rho = 0.505; Fig. 2).

4. Discussion

Herein, we showed that, similar to plants (Estrada et al., 2015), a simple dispersal measure can be used as an alternative explanation to the question why some species have larger range sizes than others. This contradicts a previous study investigating this link (Lester et al., 2007) and confirms the general notion that niche breadths are correlated with range sizes (Brown, 1984; Slatyer et al., 2013; MacLean and Beissinger, 2017).

4.1. Dispersal and range size

In general, a wide range of factors, spanning metabolic, time, risk and opportunity variables, make dispersal a costly task, either directly or indirectly (Bonte et al., 2012). Despite these costs and the fact that amphibians are considered poor dispersers due to a number of ecological factors (e.g. semipermeable skin leading to easy desiccation, habitat specificity), dispersal is important in amphibians (e.g. Funk et al., 2005; reviews by Marsh and Trenham, 2001; Smith and Green, 2005) as for most other species. Nevertheless, dispersal abilities are highly variable between and within amphibian species, e.g. ranging from 2.5 to 15 km per year in *Rhinella marina* (Marsh and Trenham, 2001) and more than 1 km in one night in *Hoplobatrachus occipitalis* (Spieler and Linsenmair, 1998). Absolute distances of individuals are naturally much higher with a recorded maximum of 34 km by *Anaxyrus fowleri* (see review by Smith and Green, 2005). However, measuring dispersal abilities is not straightforward and a simple measure is desired to circumvent the logistical problem to gather these data. We are not aware of an existing simple measure. Previous work concentrated on one method (radio-tracking, mark-recapture or genetic methods; see introduction) and did not aim at detecting universalities.

Similar to the studies on passerine birds (Laube et al., 2013) or bats (Burns and Broders, 2014), one might intuitively argue that the ratio between hind leg length (or femur length) and body length (or snout-vent length) might be a useful proxy. Certainly, frogs with longer hind legs can jump further and therefore cover long distances in a short period of time. However, it was also shown that leg muscles of jumping frogs fatigue faster than that of “walking” species (Renaud and Stevens, 1983; Chadwell et al., 2002). Thus we looked for other variables which influence dispersal. The five niche characteristics (snout-vent-length, clutch size, habitats used by adults, ecotypes of adults and habitats used by larvae; see material and methods section for their justification) used in our dispersal ability index are relatively easy to obtain for other amphibian taxa as well as for other animal groups. Additional niche characteristics, e.g. trophic level or sensitivity to isolation, are also easily implemented by adding them to equation (1). Applying the dispersal ability index to other groups might need some slight but easy to conduct modifications, e.g. maybe replacing snout-vent length by body mass if snout-vent length is difficult to obtain, standardizing clutch/litter size to reproductive output per defined time span if individual reproductive events do not take place every year. Thus, the index should be generally testable. In our case it permitted us to develop a measurement of dispersal for a group where observation data on dispersal is very scarce. So far for West African amphibians such data exists only for two species: *Hoplobatrachus occipitalis* and *Phrynobatrachus guineensis*; with completely different ecologies (*H. occipitalis*: large, aquatic, nearly ubiquitous, large range size vs. *P. guineensis*: small, terrestrial to arboreal, highly specialized, small range size). Furthermore, published dispersal data often is not comparable because of the highly different methods used, e.g. radio-tracking for *H. occipitalis* (Spieler and Linsenmair, 1998) and analysis of microsatellites in *P. guineensis* (Sandberger et al., 2010). Our dispersal ability index confirmed the former results for both species, ranking *H. occipitalis* high (3rd place, out of 176) and *P. guineensis* last. Nevertheless, at least on a small scale (less than 1.5 km maximum distance between two populations) even the small (< 20 mm SVL), highly specialized (breeding only in tiny temporary water bodies, such as tree holes or water filled snail shells), leaf litter frog *P. guineensis* seem to be highly mobile, revealing no apparent genetic structure (Sandberger et al., 2010).

Our question, whether “good dispersing species do have a wide range” can be answered positively. In addition, our study also offers an alternative explanation for the sometimes assumed direct link between larger species and larger range sizes. Though this was not observed in our case (Spearman-rank correlation, $p > 0.999$; rho (males) = 0.225; rho (females) = 0.205), it was previously reported for anurans from Australia (Murray et al., 1998) and the Brazilian Cerrado (Olalla-

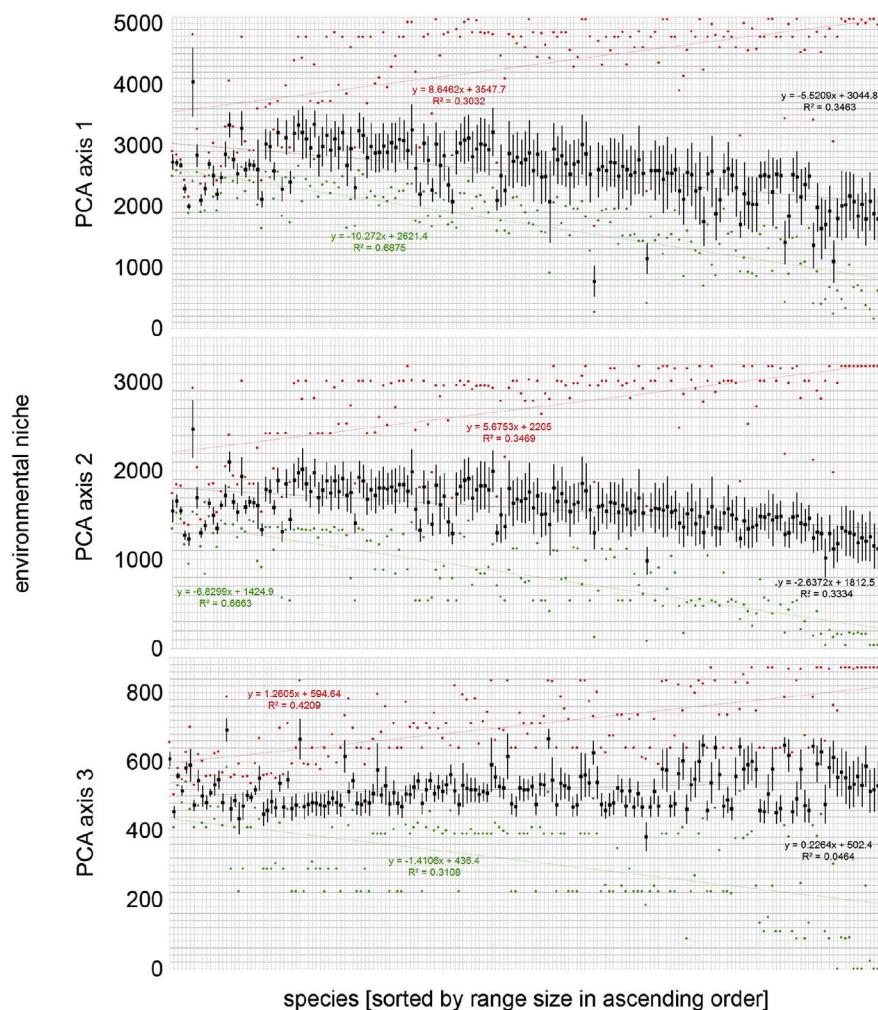


Fig. 1. Mean environmental niche breadth over the species range with variance (standard deviation), minima (green) and maxima (red). Niche breadth was measured as environmental variance, derived from a spatial PCA of 18 environmental parameters, throughout the whole range of a species. Shown are the values for three PCA axes for all 176 analyzed West African amphibian species, sorted by their range size (25–111,533,90 grid cells of 30 Arc seconds which approximate 1 km²) in ascending order (see also S1 for details). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

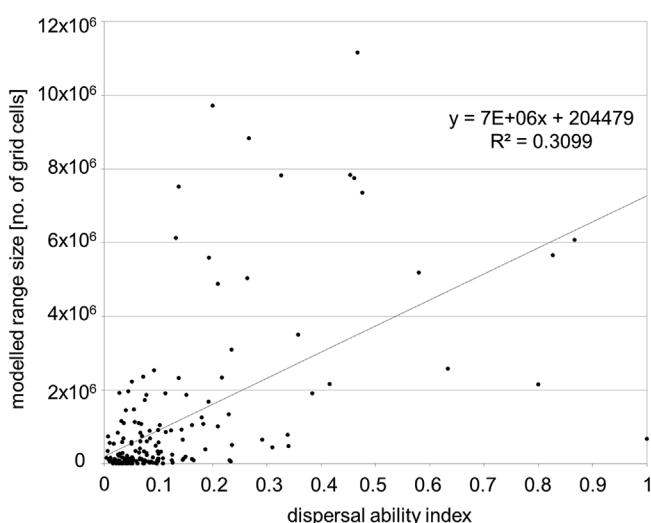


Fig. 2. Correlation between range sizes, derived from ENM, and the calculated dispersal ability index (Spearman-rank correlation, $p < 0.001$; rho = 0.496), derived from body size and habitat information (see text) for all 176 West African amphibians analyzed (see also S1 for details).

Tárraga et al., 2009) as well as a large number of other taxa ranging from plants to mammals (see review by Gaston, 2003).

4.2. Applications

The importance of our findings is twofold. First, it has implications for studies investigating the influence of climate change with the help of ENM. Currently, under different climate change scenarios and models, studies either assume no dispersal, unlimited dispersal or a previously defined limited dispersal distances ("buffers"). However, we suggest that a dispersal ability index can be used to adapt the dispersal limit of each species to each ENM run without having to measure its dispersal capabilities in the field. Another easier possibility would be to use the range size of a species as a proxy for its dispersal ability, thus adjusting the climate change ENMs individually for the range size of each species modelled.

Second, our work is important for conservation because it was already shown that a number of biological factors determine the susceptibility of amphibians to threats (Bielby et al., 2006), though these factors were not detailed or classified in the respective analysis. Thus, our results mean that amphibian species with small ranges do have low dispersal abilities, both factors contributing to their risk of extinction.

For the region West Africa our findings are especially important because it harbors a high biodiversity, not only of amphibians, which is at the same time highly threatened (Myers et al., 2000). Threats in the region, herein defined as anthropogenic disturbances are manifold and include among others (definitions after Salafsky et al., 2008; Battisti et al., 2016): residential and commercial developments, agriculture and

aquaculture, energy production and drilling, human intrusions and disturbances. The importance of climate change and severe weather remains unclear. The main large scale consequences are habitat alterations, especially the large scale fragmentation of forests (Mayaux et al., 2004, 2013; Hansen et al., 2013). For the majority of species it remains also unclear what the effects of fragmentation are and how they interact, see Ewers and Didham (2006) for a review on confounding factors. In general, as elsewhere, some generalist species seem to profit from habitat alterations and fragmentations (e.g. in West Africa *Sclerophrys regularis*, *Hoplobatrachus occipitalis*) and species specialized on primary forests seem to disappear (e.g. *Sclerophrys taiensis*, *Afrixalus vibekensis*; Ernst and Rödel, 2005; Ernst et al., 2006). In leaf litter anurans the distance to large continuous tracts of forest seem be important (Hillers et al., 2008).

Thus for regional conservation plans a comprehensive overview is required. In our opinion, this has to include assessing the current status of biodiversity, identifying the main threats and develop different models of the potential future. Than the urgently needed political decisions can be made to safeguard unique places on the globe, such as the West African forests.

Authors' contribution

JP designed the study, analyzed the data and wrote the first draft of the paper. JP and MOR collated the data and worked on all subsequent versions of the paper. Both authors approved the final version.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2017.11.011>.

References

- Austin, J.D., Dávila, J.A., Lougheed, S.C., Boag, P.T., 2003. Genetic evidence for female-biased dispersal in the bullfrog, *Rana catesbeiana* (Ranidae). *Mol. Ecol.* 12, 3165–3172.
- Battisti, C., Poeta, G., Fanelli, G., 2016. An Introduction to Disturbance Ecology - a Road Map for Wildlife Management and Conservation. Springer International Publishing, Switzerland.
- Beck, C.W., Congdon, J.D., 2000. Effects of age and size at metamorphosis on performance and metabolic rates of southern toad, *Bufo terrestris*, metamorphs. *Funct. Ecol.* 14, 32–38.
- Berven, K.A., Grudzien, T.A., 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution* 44, 2047–2056.
- Bielby, J., Cunningham, A.A., Purvis, A., 2006. Taxonomic selectivity in amphibians: ignorance, geography or biology? *Anim. Conserv.* 9, 135–143.
- Blaustein, A.R., Wake, D.B., Sousa, W.P., 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conserv. Biol.* 8, 60–71.
- Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V.M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T.G., Chaput-Bardy, A., Clober, J., Dytham, C., Hovestadt, T., Meier, C.M., Palmer, S.C.F., Turlure, C., Travis, J.M.J., 2012. Costs of dispersal. *Biol. Rev.* 87, 290–312.
- Breden, F., 1987. The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, *Bufo woodhousei Fowleri*. *Copeia* 1987, 386–395.
- Brown, J.H., 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124, 255–279.
- Burns, L.E., Broders, H.G., 2014. Correlates of dispersal extent predict the degree of population genetic structuring in bats. *Conserv. Genet.* 15, 1371–1379.
- Chadwell, B.A., Hartwell, H.J., Peters, S.E., 2002. Comparison of isometric contractile properties in hindlimb extensor muscles of the frogs *Rana pipiens* and *Bufo marinus*: functional correlations with differences in hopping performance. *J. Morphol.* 251, 309–322.
- Chase, J.M., Leibold, M.A., 2003. Ecological Niches, Linking Classical and Contemporary Approaches. The University of Chicago Press, Chicago, USA.
- Chelgren, N.D., Pearl, C.A., Adams, M.J., Bowerman, J., 2008. Demography and movement in a relocated population of Oregon spotted frogs (*Rana pretiosa*) - influence of season and gender. *Copeia* 2008, 742–751.
- Dole, J.W., 1971. Dispersal of recently metamorphosed leopard frogs, *Rana Pipiens*. *Copeia* 1971, 221–228.
- Duellman, W.E., Trueb, L., 1994. Biology of the amphibians. The John Hopkins University Press, Baltimore, USA.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.C., Peterson, A.T., Phillips, S.J., Richardson, K., Schachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmerman, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. *Divers. Distributions* 17, 43–57.
- Ernst, R., Rödel, M.-O., 2005. Anthropogenically induced changes of predictability in tropical anuran assemblages. *Ecology* 86, 3111–3118.
- Ernst, R., Linsenmair, K.E., Rödel, M.-O., 2006. Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. *Biol. Conserv.* 133, 143–155.
- Estrada, A., Meireles, C., Morales-Castilla, I., Poschlod, P., Vieites, D., Araújo, M.B., Early, R., 2015. Species' intrinsic traits inform their range limitations and vulnerability under environmental change. *Glob. Ecol. Biogeogr.* 24, 849–858.
- Estrada, A., Morales-Castilla, I., Caplat, P., Early, R., 2016. Usefulness of species traits in predicting range shifts. *Trends Ecol. Evol.* 31, 190–203.
- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* 81, 117–142.
- Funk, W.C., Greene, A.E., Corn, P.S., Allendorf, F.W., 2005. High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. *Biol. Lett.* 1, 13–16.
- Gaston, K.J., 2003. The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford, UK.
- Goater, C.P., Semlitsch, R.D., Bernasconi, M.V., 1993. Effects of body size and parasite infection on the locomotory performance of juvenile toads, *Bufo Bufo*. *Oikos* 66, 129–136.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehmann, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, L.R.G., 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342, 850–853.
- Heikkilä, R.K., Marmion, M., Luoto, M., 2012. Does the interpolation accuracy of species distribution models come at the expense of transferability? *Ecography* 35, 276–288.
- Herkt, K.M.B., Barnikel, G., Skidmore, A., Fahr, J., 2016. A high-resolution model of bat diversity and endemism for continental Africa. *Ecol. Model.* 320, 9–28.
- Hillers, A., Veith, M., Rödel, M.-O., 2008. Effects of forest fragmentation and habitat degradation on West African Leaf-litter frogs. *Conserv. Biol.* 22, 762–772.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harb. Symposia Quantitative Biol.* 22, 415–427.
- Jameson, D.L., 1956. Growth, dispersal and survival of the Pacific tree frog. *Copeia* 1956, 25–29.
- Lampert, K.P., Rand, A.S., Mueller, U.G., Ryan, M.J., 2003. Fine-scale genetic pattern and evidence for sex-biased dispersal in the túngara frog, *Physalaemus Pustulosus*. *Mol. Ecol.* 12, 3325–3334.
- Laube, I., Korntheuer, H., Schwager, M., Trautmann, S., Rahbek, C., Böhning-Gaese, K., 2013. Towards a more mechanistic understanding of traits and range sizes. *Glob. Ecol. Biogeogr.* 22, 233–241.
- Leibold, M.A., 1995. The niche concept revisited: mechanistic models and community context. *Ecology* 76, 1371–1382.
- Lester, S.E., Ruttenberg, B.I., Gaines, S.D., Kinlan, B.P., 2007. The relationship between dispersal ability and geographic range size. *Ecol. Lett.* 10, 745–758.
- MacLean, S.A., Beissinger, S.R., 2017. Species' traits as predictors of range shifts under contemporary climate change: a review and meta-analysis. *Glob. Change Biol.* <http://dx.doi.org/10.1111/gcb.13736>.
- Marsh, D., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. *Conserv. Biol.* 15, 40–49.
- Mayaux, P., Bartholomé, E., Fritz, S., Belward, A., 2004. A new land-cover map of Africa for the year 2000. *J. Biogeogr.* 31, 861–877.
- Mayaux, P., Pekel, J.-F., Desclée, B., Donnay, F., Lupi, A., Achard, F., Clerici, M., Bodart, C., Brink, A., Nasi, R., Belward, A., 2013. State and evolution of the African rainforests between 1990 and 2010. *Philosophical Trans. R. Soc. B* 368, 20120300.
- Morrison, C., Hero, J.-M., 2003. Geographic variation in life-history characteristics of amphibians: a review. *J. Animal Ecol.* 72, 270–279.
- Murray, B.R., Fonseca, C.R., Westoby, M., 1998. The macroecology of Australian frogs. *J. Animal Ecol.* 67, 567–579.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., DaFonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403 853–845.
- Olalla-Tárraga, M.A., Diniz-Filho, A.F., Bastos, R.P., Rodríguez, M.A., 2009. Geographic body size gradients in tropical regions: water deficit and anuran body size in the Brazilian Cerrado. *Ecography* 32, 581–590.
- Palo, J.U., Schmeller, D.S., Laurila, A., Primmer, C.R., Kuzmin, S.K., Merilä, J., 2004. High degree of population subdivision in a widespread amphibian. *Mol. Ecol.* 13,

- 2631–3644.
- Penner, J., Wegmann, M., Hillers, A., Schmidt, M., Rödel, M.-O., 2011. A hotspot revisited - a biogeographical analysis of West African amphibians. *Divers. Distributions* 17, 1077–1088.
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Phillips, S.J., Dudík, M., Schapire, R.E., 2004. In: Brodley, C. (Ed.), A Maximum Entropy Approach to Species Distribution Modeling. Proceedings of the Twenty-first International Conference on Machine Learning. ACM Press, New York, pp. 655–662.
- Pigot, A.L., Owens, I.P.F., Orme, C.D.L., 2012. Speciation and extinction drive the appearance of directional range size evolution in phylogenies and the fossil record. *PLoS Biol.* 10, e1001260.
- R Core Team, 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria Available at: <http://www.R-project.org/>.
- Renaud, J.M., Stevens, E.D., 1983. A comparison between field habitats and contractile performance of frog and toad sartorius muscle. *J. Comp. Physiology* 151, 127–131.
- Rizopoulos, D., 2006. ltm: an R package for latent variable modelling and item response theory analyses. *J. Stat. Softw.* 17, 1–25.
- Rothermel, B.B., Semlitsch, R.D., 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conserv. Biol.* 16, 1324–1332.
- Salafsky, N., Salzer, D., Stattersfield, A.J., Hilton-Taylor, C., Neugarten, R., Butchart, S.H.M., Collen, B., Cox, N., Master, L.L., O'Connor, S., Wilkie, D., 2008. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. *Conserv. Biol.* 22, 897–911.
- Sandberger, L., Feldhaar, H., Lampert, K.P., Lamatsch, D.K., Rödel, M.-O., 2010. Small, specialised and highly mobile? The tree-hole breeding frog, *Phrynobatrachus guineensis*, lacks fine-scale population structure. *Afr. J. Herpetology* 59, 79–94.
- Schorr, G., 2003. Die Amphibiengemeinschaften auf Inselbergen im Taï-Nationalpark, Côte d'Ivoire, Westafrika - Gemeinschaftsökologische und inselbiogeographische Aspekte. Diploma thesis. University of Würzburg, Würzburg, Germany.
- Semlitsch, R.D., 1981. Differentiating migration and dispersal processes for pond-breeding amphibians. *J. Wildl. Manag.* 72, 260–267.
- Sinsch, U., 1990. Migration and orientation in anuran amphibians. *Ethol. Ecol. Evol.* 2, 65–69.
- Slatyer, R.A., Hirst, M., Sexton, J.P., 2013. Niche breadth predicts geographical range size: a general ecological pattern. *Ecol. Lett.* 16, 1104–1114.
- Smith, M.A., Green, D.M., 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* 28, 110–128.
- Spieler, M., Linsenmair, K.E., 1998. Migration and diurnal shelter in a ranid frog from a West African savannah: a telemetric study. *Amphibia-Reptilia* 19, 43–64.
- Szymura, J.M., Barton, N.H., 1991. The genetic structure of the hybrid zone between the fire-bellied toads *Bombina bombina* and *B. variegata*: comparisons between transects and between loci. *Evolution* 45, 237–261.
- Trakimas, G., Whittaker, R.J., Borregaard, M.K., 2016. Do biological traits drive geographical patterns in European amphibians? *Glob. Ecol. Biogeogr.* 25, 1228–1238.
- Vieites, D.R., Wollenberg, K.C., Andreone, F., Köhler, J., Glaw, F., Vences, M., 2009. Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proc. Natl. Acad. Sci.* 106, 19715–19722.